10464

Fungus-Growing Ants

Neal A. Weber

Reprinted from Science, August 5, 1966, Vol. 153, No. 3736, pages 587-604

Fungus-Growing Ants

A symbiotic relationship exists between an insect and a plant, involving an effective culturing technique.

Neal A. Weber

The fungus-growers are a New World tribe of myrmicine ants, the Attini, that has developed a unique relation with saprophytic plants. The ants eat only the fungus that they culture, and it is not found outside the ant nest. Many animals feed on fungi, and certain beetles and termites grow them in their nests, but the culturing of fungi as described here is believed to be unique. In this process a flourishing growth of one fungus is produced, and of this fungus only, although the medium on which it grows (the substrate) is suitable for the growth of many other kinds of organisms. When the ants are removed, these other organisms multiply and replace the fungus.

The vital part of the attine nest is the fungus garden. It is the abode of the queen and brood as well as of the fungus. Despite the diversity in morphology of the species, the development and care of the garden are fundamentally similar for all varieties.

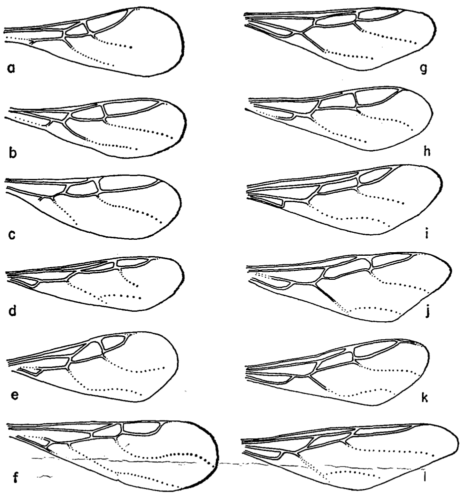
Fungus-growing is distinguished from leaf-cutting. All members of this tribe subsist solely, in nature, on the fungus that they culture, but some are leaf-cutters and others are not. The latter pick up vegetal particles of suitable size, or insect excrement, and grow the fungus on these. The leaf-cutters go in files, often on well-formed trails, and cut leaves, flowers, or stems. They are most commonly members of the largest species and belong to the genera *Acromyrmex* and *Atta*. Inconspicuous *Trachymyrmex* and *Sericomyrmex* species may also cut leaves and flowers.

It is the purpose of this article to review the chief features of the life of these ants and of the fungus on which they depend. Because of the economic importance of the large species of *Atta*, and particularly of *Atta sexdens* L. in Brazil, a considerable body of literature has grown up, here summarized, and *A. sexdens* may be taken to represent a high expression of this symbiosis. Studies of other species and genera have made significant contributions to the knowledge of the biological role of the attines and are here reviewed.

Species of this tribe were listed by Linnaeus in 1758, and the type genus *Atta* was named by Fabricius in 1804. Latreille called such ants *Oecodoma* in 1818, and this name was used by the early naturalists, such as Bates, Belt, and Smith in Latin America, for the conspicuous leaf-cutters with soldiers now known as *Atta*. Mayr, from 1862 to 1865, originated the generic names *Cyphomyrmex*, *Apterostigma*, *Sericomyrmex*, and *Acromyrmex*, and he has been the chief contributor to the generic classification. Outlines of the wings, heads, and side views of the ants show differences characteristic of the genera (Figs. 1–4).

The tribe has a wide distribution, from approximately 40° north latitude to 44° south latitude (Fig. 5). The economically important *Atta* species have smaller ranges (Figs. 6 and 7). Their general distribution in South

The author is professor of zoology, Swarthmore College, Swarthmore, Pennsylvania.

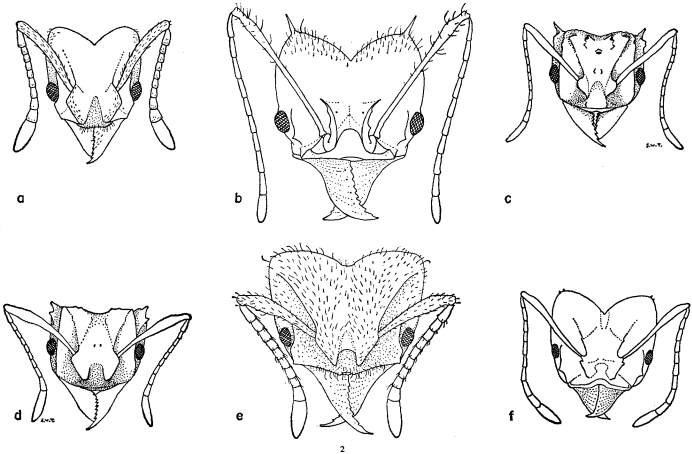


American countries is known, although incompletely in Andean areas.

Thomas Belt, who arrived in Nicaragua in 1868, discovered the fungus-growing role of the ants (*1*). He did not realize the full extent of the ant-fungus relationship, thinking that the fungus grew naturally in the damp underground chambers of the ant nest. Belt greatly stimulated Alfred Moeller (*2*), who quoted Belt's conclusions on the frontispiece of his publication.

Fig. 1 (left). Wings of representative genera. (*a*) *Cyphomyrmex rimosus Spinola.* (*b*) *C. bigibbosus* Emery. (*c*) *Mycetophylax conformis.* (*d*) *Mycocepurus manni Weber.* (*e*) *Myrmicocrypta buenzlii* Borgmeier. (*f*) *Apterostigma robustum* Emery. (*g*) *Sericomyrmex urichi.* (*h*) *Trachymyrmex cornetzi* Forel. (*i*) *T. urichi* Forel. (*j*) *Acromyrmex (Moellerius) landolti pampanus* Weber. (*k*) *A. (A) octospinosus* Reich. (*l*) *Atta sexdens.*

Fig. 2 (below). Outline of heads of representative species of genera (head length includes mandibles). (*a*) *Mycetophylax conformis* (Mayr); head 0.89 mm. (*b*) *Atta cephalotes opaca* Forel; head 4 mm. (*c*) *Trachymyrmex jamaicensis* E. André; female head 1.8 mm (*d*) *T. jamaicensis*; worker head 1.5 mm. (*e*) *Sericomyrmex urichi* Forel; head 1.5 mm. (*f*) *Acromyrmex (Moellerius) landolti* Forel; head 2.2 mm.



Moeller and then von Ihering, Sampaio, Goeldi, and Huber (*3, 4*) showed the dependence of the ants on the fungus and how this dependence was transmitted from one ant generation to another. Moeller first produced evidence that there could be a fungus sexual or fruiting stage; to this stage he gave the name *Rozites gonglyophora*. His careful mycological studies were basic to later work.

Specimens of *Atta cephalotes* L. and *A. sexdens* had been brought from Guiana to Europe in the 18th century. Their long trails, thronged with workers, had been confused with the files of army ants, *Eciton*, in the popular accounts brought back to Europe from Tropical America. The ants also figured in Central American mythology (*5*).

Almost as soon as the Spanish arrived in the New World they made note of the depredations of ants, which probably were *Acromyrmex* or *Atta*. Bartolome de las Casas in 1559 described the failure of the Spaniards in Hispaniola to grow cassava and citrus trees because of ants whose nests, at the bases of the trees, were "white as snow" (probably the fungus gardens and brood). Article 19 of the cedula proclaimed by the King of Spain on 20 November 1783 for opening Trinidad to immigration states that "the Government was to take the utmost care to prevent the introduction of ants into Trinidad" (see *6*). The ants, of course, had been there all along.

The importance and conspicuousness of *Atta* are attested by the common names which are in general use by the people of various Latin-American countries and used in official publications by their ministries or departments of agriculture (*7*).

Latin-American countries have passed national laws classifying certain ant species as plague animals because of their concentration on economically important plants. For example, Argentina, in Law 4863 of 27 July 1909, considered "*hormigas coloradas*" and "*hormigas negras*" to be plagues. These were later identified as *Atta sexdens* and *Acromyrmex lundi* (Guer.). When the ants are legally classified among the plague animals, the government usually undertakes to carry out extermination methods at the expense of the person occupying or owning the land, if he does not do it himself. The government also surveys yearly the incidence of the animals and the damage done by them and freely disseminates the information. In many countries experts experiment with all control products as they are developed (*8, 9*). A method of controlling *Atta* that is effective in one country will have a calculable probability of success against *Atta* in another country, based on differences in soil, climate, and other variables. No one product has had such complete success in any country that it has replaced all other control methods for very long. People still have difficulty in practicing agriculture in some primitive areas (see *10*).

The Indians of Central and South America have long used the large females of *Atta* as food, and there is no doubt that the gasters filled with eggs have nutritional value. I tried them raw and found them to have a pasty consistency and a bland flavor.

Of even greater importance is the impact of these ants on soil nutrition (*11*). In tropical rain forest areas few animals and few roots of trees go much below the soil surface. In such sites a large *Atta* nest contains far more organic matter, in the form of hundreds of fungus gardens, than any other agency in the soil. This organic matter makes possible the multiplication of great quantities of bacteria, nematodes, insects, and other organisms that can only exist deep underground in such numbers because the ants have carried substrate there.

More pervasive, if less dramatic, is the influence of the nests of smaller and less conspicuous attines. Recent studies of these species in Trinidad showed that there was an average of a nest every 2 square meters in one area (*12*). The size and numbers of the fungus gardens showed that the total impact of these ants on soil nutrition was considerable. They were the only burrowers in the area to construct large underground chambers. These were filled with gardens, as in *Atta*. On the fertile pampas of Argentina the presence of nests of *Acromyrmex* is marked above ground by a richer growth of plants (*11*).

Atta sexdens

The best known and economically most important South American attine is *Atta sexdens* L., together with its subspecies *A. rubropilosa* Forel. This has been the species most commonly studied in Brazil.

Huber (*3*) observed in detail the early stages of colony foundation and watched the female, larvae, and first brood consuming the eggs that she had laid. He estimated that 90 percent of the eggs laid in the approximately 40 to 60 days before the first workers appear were consumed; about 50 eggs were laid daily in this period. Among these Autuori (*13*) clearly distinguished eggs of two kinds, alimentary and reproductive, and he produced an excellent photographic record. The alimentary eggs, laid in the early stages of colony formation, are markedly larger and more globular than the reproductive eggs. The female eats the alimentary eggs herself or feeds them to the first larvae. The internal anatomy of the female gaster (*14*) and the histological basis for the two egg types (*15*) have been described. The spermatheca of the newly fertilized female has been shown to contain some 200 to 300 million sperm as a result of probable fertilization by from three to eight males (*16*).

Autuori has also graphically portrayed the reproductive potential and size of mature nests.

In five successive years the nuptial flights and preparation of the initial nest of the females were noted, then the emergence of the first workers. The average interval between the nuptial flight and the emergence of these workers was 87.2 days, varying from 72.0 days in 1938 to 93.9 days in 1937. Temperatures must have been a significant factor in the time required for development, and Eidmann (*14*) gives these as 18.5° to 25.3°C in the mature garden, according to the depth. The workers used the original nest opening first made by the female.

From examination of a number of young colonies, the average developmental times were found to be as follows: pre-oviposition period, 5 days; incubation, 22 days; larval period, 22 days; pupal period, 10 days.

The appearance of a second nest opening marked the next significant stage. This took place, on the average, 443 days after the appearance of the first opening (minimum 421, maximum 561 days).

The full size range of worker castes appeared between the 4th and 10th month, the soldier caste not appearing until the 22nd month.

The number of entrances to the nests rapidly increased in the second year to 63, 113, and 53, respectively, in three colonies. In the 38th month the numbers had increased to 853, 984, and 1071, respectively. Betan-

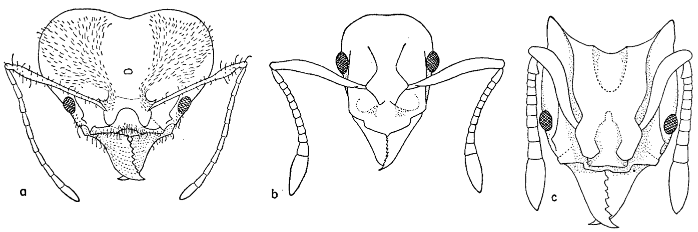


Fig. 3. Outline of heads of representative species of genera (head length includes mandibles). (*a*) *Atta cephalotes opaca*; soldier head 5.8 mm. (*b*) *Apterostigma calverti* Wheeler; head 1.6 mm. (*c*) *Cyphomyrmex bigibbosus* Emery; head 1.3 mm.

court *(17)* used the data in estimating the size of the colony. He maintained that the numbers of openings can be plotted as a logistic curve

$$N = \frac{1000}{271737e - 0.42\ t + 1}$$

where N = monthly average total openings, e = natural logarithmic base, t = number of months from the start of nest building, and 1000 = the theoretical upper asymptote. The maximum size of 1000 openings approximately coincides with the beginning of the production of sexual forms.

A nest of 47 months was opened by Autuori on the day before its second nuptial flight. This nest had 1027 chambers, of which 390 had fungus gardens and ants. There were 38,481 males and 5339 females, a proportion of males to females of 7.2 to 1 [Eidmann *(14)* had given the ratio as 10:1]. An enormous chamber at a depth of 125 centimeters was used as a refuse site and cemetery. It was 90 centimeters high and 120 centimeters in diameter. This contained 1491 adult Coleoptera, 15 adult Diptera, 56 Hemiptera, 40 Mollusca, 4 Reptilia, and 1 Pseudoscorpionida.

Autuori followed one nest for 77 months. It produced a nuptial flight

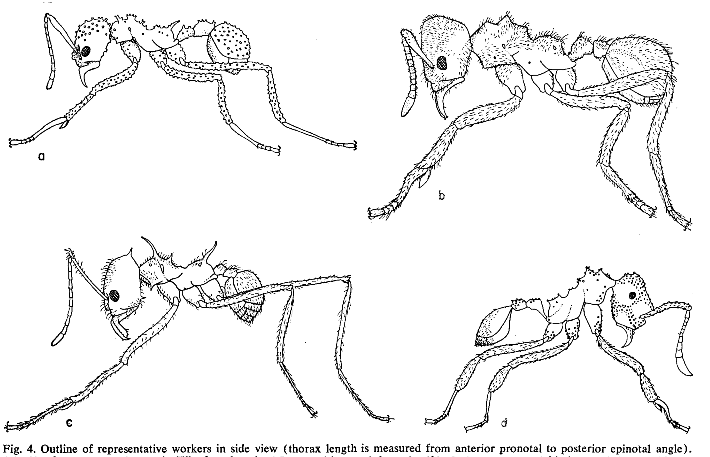


Fig. 4. Outline of representative workers in side view (thorax length is measured from anterior pronotal to posterior epinotal angle). (*a*) *Trachymyrmex arizonensis* Wheeler; length 4.5 mm (thorax 1.6 mm). (*b*) *Sericomyrmex urichi*; length 3.5 mm (thorax 1.5 mm). (*c*) *Atta cephalotes opaca*; length 7 mm (thorax 2.8 mm). (*d*) *Myrmicocrypta ednaella* Mann; length 2.3 mm (thorax 0.85 mm).

in its third year and annually thereafter. The loose soil on the surface of the nest was measured before the nest was excavated; it amounted to 22.72 cubic meters and weighed approximately 40,000 kilograms. There were 1920 chambers in this nest, 296 containing refuse, 157 with loose soil, 248 with gardens, and 1219 empty. The empty chambers were believed to have been used for sheltering the sexual forms after they matured and before they left on their nuptial flight. The weights of 184 fungus gardens varied from 15 to 2250 grams, a common weight being 300 grams. It was calculated that, during the life of the colony, 5892 kilograms of vegetation had been used in the nest, with an estimated ratio of 12.4 parts fresh substrate to 1 part discarded substrate.

The mortality of females following their nuptial flight was determined by excavating the nest sites after the resulting colonies had opened the entrance. Autuori concluded that as many as 97.5 percent of the queens died within 100 days. Of the young nests, 99.95 percent were destroyed by natural causes within 15 months. The critical period in colony life was divided into four phases: (i) descent from nuptial flight to ground, 30 to 60 minutes; (ii) excavation of the tunnel and first chamber, 6 to 8 hours; (iii) queen remains in chamber, rearing first brood, 80 to 100 days; (iv) from opening of first entrance to opening of second, 15 months.

Mammals, birds, and other insects, including other genera of ants, were significant predators.

In a later study it was concluded that it was impossible to rid extensive areas of *Atta* colonies. The best that could be expected was the eradication of nests in limited areas that could be thoroughly examined every 3 to 6 months.

Second in importance in Brazil and of primary importance northward to tropical Mexico is *Atta cephalotes*. Where the ranges of the two come together, in Surinam (*18*), British Guiana (*19*), Venezuela (*10*), Peru (*20*), and Panama (*21*), the species show ecological differences, *A. cephalotes* often inhabiting more densely forested areas.

The nests of *Atta cephalotes* are similar to those of *A. sexdens*. There is an extensive system of canals to permit air exchange, with one or more very large chambers (*Abraumgruben*), a meter or more in height, that may be used for refuse. Of 75 fungus gardens found in a mature nest, 44 weighed between 100 and 300 grams (*18*). In appearance, the gardens and the fungus are identical to those of *A. sexdens*. The trails may be well developed (Fig. 8).

Recent studies of young colonies of *A. cephalotes* of known age in Trinidad permit a cataloging of the stages (*12*). These stages show an acceleration in development over those for *A. sexdens* in South Brazil (*22*), due probably to somewhat higher temperatures and higher rainfall. In Trinidad the temperature was 25° to 26°C at the 10- to 50-centimeter depths, under shade, where the young colonies were located (*23*).

Atta cephalotes Nest Stages

Stage 1. The reopening of the initial tunnel made by the female is marked at first by a scattering of soil grains about the entrance, then by the formation of a low tumulus or crater that is often 5 to 8 centimeters in diameter. Trail-making activity starts. Stage duration, 1st and 2nd months (see *10*, plate 2; *22*).

Stage 2. Externally the nest has a small turret of soil grains (10 to 15 centimeters high) and can be distinguished from turrets of other insects and other animals by the large size of the opening. There is a single underground chamber at first, then a second may be started. Only the smallest-to-medium-sized workers are produced. Small trails may extend in all directions. Duration, 2nd to 4th month (see *24*, Figs. 1 and 2; *22*).

Stage 3. The original chimney has now grown to a crater or cone because of the increase in amount of soil excavated. There is still only one entrance. The soil is dumped in the immediate vicinity of the original opening. The two underground chambers are increased to three or four. By this time the colony consists of several thousand workers, some of which are small soldiers. Fewer and more definite trails are formed. Duration, 4th to 7th month.

Stage 4. The number of craters is increased from one to two or three or more. None of these is a turret; they are, rather, low craters of the type many ant species construct, except for their size, 20 to 40 centimeters in diameter. Each crater surrounds an entrance to the nest. Full-size soldiers are being produced. Duration, 7th to 11th month.

Stage 5. A score or two of craters, and a corresponding number of entrances and fungus gardens (similar to those of *A. sexdens*), characterize a fifth stage. Duration, 11th to 16th month.

Stage 6. From now on the colony increases to hundreds of thousands of workers. Sexual broods are produced annually at the appropriate season. Many scores of craters and fungus gardens are developed. It is this mature stage that has been well described in South America and Louisiana (*13, 14, 18, 25, 26*) (Figs. 9 and 10) for several *Atta* species.

The nests of the other species of *Atta* are known chiefly in their mature phases. Those of *A. vollenweideri* and *A. laevigata* in Argentina have been described (*26, 27*). The nest of the Panamanian *A. colombica tonsipes* Santschi is much like that of *A. cephalotes isthmicola* Weber in the same forest (*21*).

General Characters of Attines

Anatomical features that are significant in the life of all fungus-growers include the adult mouthparts, essential to grooming and feeding on the fungus, the infrabuccal pocket that receives dirt from the grooming as well as strands of the fungus, and the pecten or comb used in grooming (*28*; see also *10, 29*) (Fig. 11). Males, females, and workers all use those structures throughout their adult life.

If the ants found in files are strongly polymorphic, they belong to *Acromyrmex* or *Atta*. Characteristically the size range of the worker is continuous, from the smallest, or minima caste, through a series of castes of intermediate size, or media, to the largest, or maxima caste. The extreme in the nonreproductive of *Atta* is usually called the soldier caste and has a disproportionately large head. Such an *Atta* size series (Fig. 12) then would be: (i) minima (total body length, 2 millimeters); (ii) media; (iii) maxima, including soldier caste (total body length, 14 millimeters).

The first two are the only worker castes found in *Atta* nests in the first several months of colony life. A few workers of the maxima sizes are produced during the first 6 months in *Atta cephalotes*, then an occasional soldier will appear (*30*). A large number of soldiers characterizes a mature colony.

The castes of *Atta* and *Acromyrmex* show a division of labor. The minima are largely confined to the fungus gardens and are effective in culturing the fungus and caring for the eggs and small larvae. The minima are so closely attached to the garden that, if a piece of the latter is removed, the minima flatten closely to the irregularities and do not leave the fragment. Workers of the media sizes also tend the gardens and brood, but in addition they cut leaves. The maxima cut leaves and protect the colony. The *Atta* soldiers tend to remain in the garden, often in the vicinity of the queen and brood, and come out mostly when the nest is disturbed. Their mandibles will, with one cut, produce a 5-millimeter cut in human skin; they can cut half-moon sections out of one's leather shoes.

The species of the other attine genera are largely monomorphic. There may be feeble polymorphism in such *Trachymyrmex* as *T. urichi* and *T. septentrionalis*. Laboratory colonies of these, especially of *T. septentrionalis*, may rear progressively smaller workers as the colony deteriorates or, in the latter species, after the height of summer brood raising.

Communication among the members of a colony is accomplished by various means. Studies at the turn of this century indicated that stridulation is an important factor in maintaining cooperation between widely separated ants in underground chambers and that the vibrations are perceived by the ants through the soil (*5*). Recently these vibrations in *Atta cephalotes* have been clearly recorded (*31*).

Tactile communication is indicated whenever two ants of a colony meet. In all species the ants advance with antennae widespread and directed toward the other ant. Then the apices of the antennae meet, and the ants may maintain this position for a second or two, then continue with their previous activities. If the ants are of different species they merely approach without touching antennal apices, then generally act hostile. In these cases the responses may be chemical.

Wilson has shown that the general method of communication is chemical (*32*). The number and complexity of the chemicals are now being effectively studied. The general term for these substances is pheromone, defined as a chemical signal used in communication among members of the same species. He recognizes, among ants generally nine categories of responses: alarm, simple attraction, recruitment, grooming, exchange of oral and anal liquid, exchange of solid food particles, facilitation, recognition, and caste determination. My observations of numerous attine species indicate that, of these nine, the first four and the last three are the usual responses. A further modification of the chemicals would enable the ants to distinguish their own colony mates from other members of the same species.

A special use of pheromones is their use in making a scent trail (*33*). Ants of several attine species have been shown to follow one another by this means. The ants deposit droplets at intervals. These droplets form the trail, and other ants follow. The trail, in nature, may be invisible to the human eye, as reported for *Trachymyrmex isthmicus* (*21*). An alarm pheromone in mandibular glands of *Atta sexdens rubropilosa* has been isolated (*34*).

Visual means of communication have been little studied. Workers and soldiers of *Atta* will respond to a waving of the finger on the outside of the glass or plastic tube in which they are confined. Both males and females, especially males, have large eyes, and it seems possible that it may be a combination of chemical, auditory, and visual stimuli which brings the sexes together in the nuptial flight.

The Brood

The attine brood is normally covered by the mycelium of the garden, contrary to the impression given by photographs of the brood in the early

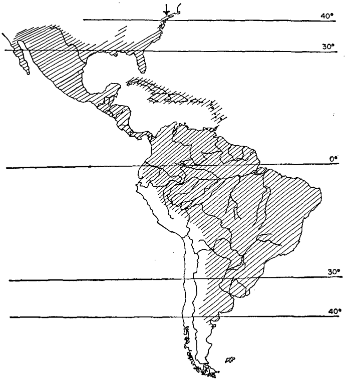


Fig. 5. Distribution of *Attini.*

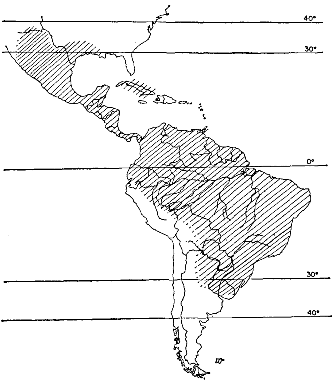


Fig. 6. Distribution of *Atta.*

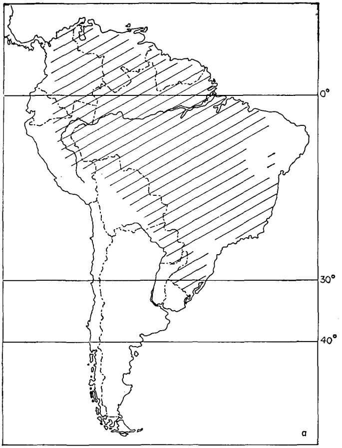


Fig. 7. Distribution of four species of *Atta* in South America [Brazilian distribution after Gonçalves (9)]. (*a*) *A. sexdens* L. The species is also found in the western and drier part of Panama. (*b*) *A. laevigata* F. Smith, a species found in the drier part of South America. (*c*) *A. vollenweideri* Forel, a species confined to southcentral parts of the continent. (*d*) *A. cephalotes* L. The species also extends through Central America into Mexico.

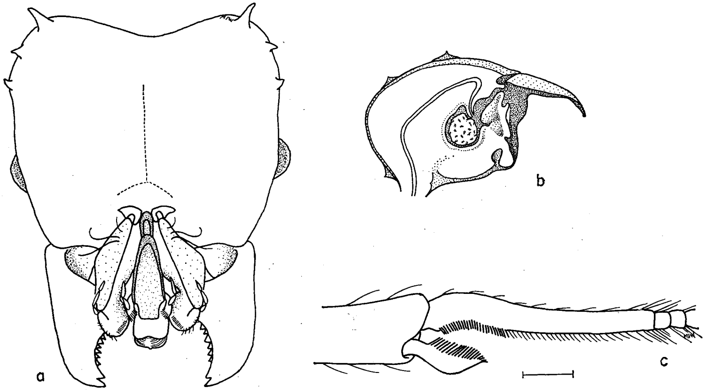


Fig. 11. Significant anatomical features. (*a*) Mouthparts of *Acromyrmex lundi* (Guérin), from behind, showing the extended central tongue or hypopharynx. (*b*) Sagittal section of *Atta* head, showing the infrabuccal pocket in the rear of the mouth. It contains a fungal mass that will be the nucleus for the new garden when the female leaves the parental nest [after Huber]. (*c*) Part of the foreleg of an *Atta* worker, showing the pecten used for cleaning the appendages. The bar represents 0.25 millimeter.

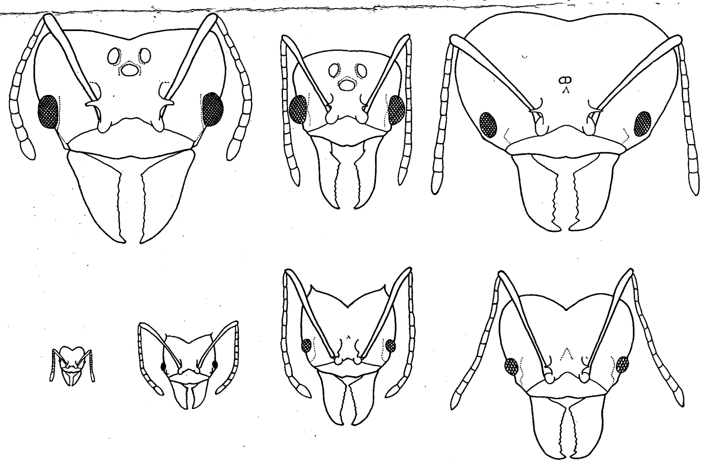
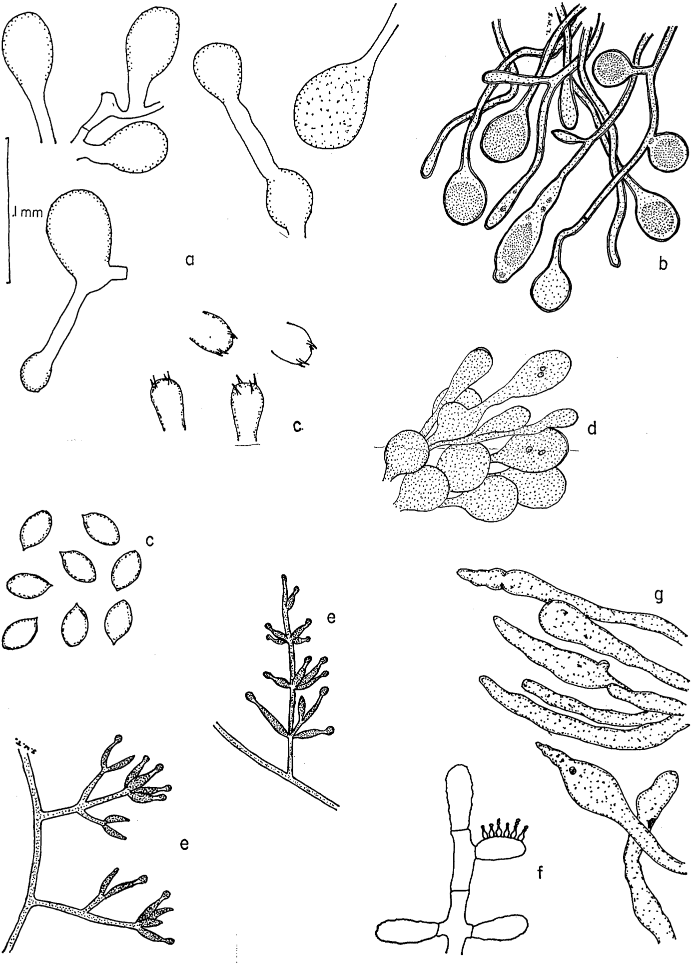


Fig. 12. *Atta cephalotes*. Outline of heads of castes, to scale. Lengths include the mandibles; width between eyes, in millimeters, given in parenthesis. (Top row, left to right) Female, 5.8 mm (3.92); male, 4.1 mm (2.28); soldier, 5.8 mm (3.54). (*Bottom* row left to right) Minima worker, 0.9 mm (0.58); media worker, 1.8 mm (1.16); media worker, 3.5 mm (2.03); maxima worker, 4.3 mm (2.53).



1 mm
a
b
c
d
c
e
g
e
f

ter yet—his sporophores can be produced in artificial culture from the stage present in the normal nest. Forel referred to ants sowing spores; if spores are produced the ants never sow them but abandon that part of the nest. Forel's statement that indigenous vegetation (as contrasted with exotics), "gradually reinforced by natural selection, resists the attacks" of the ants does not correspond with the situation. His dismissal, as a myth, of the story of carpets of green leaf sections in garden chambers was premature. Such carpets may be found after times of abundant leaf-cutting.

The Fungus

Fungi associated with attine ants have been given a number of names since Moeller described the first one as *Rozites gonglylophora* in 1893. A review appeared in 1938 (*46*). These fungi included *Xylaria, Bargellinia, Rhizomorpha, Locellinia, Poroniopsis, Lentinus,* and *Tyridiomyces* (Fig. 29) species belonging to the Ascomycetes, Basidiomycetes, and Fungi Imperfecti.

The assumption by investigators (*13, 18*) that the fungus grown by other *Acromyrmex* and *Atta* was the same as Moeller's *Rozites gonglylophora* of *Acromyrmex disciger* was challenged by Jacoby (*22*). The fungi are superficially much alike, as cultured by the ants, but Jacoby's experiments in which he exchanged gardens of the two fungus species resulted in rejection of each. I had performed this type of experiment earlier, in 1934–35 (*19, 37*), with many Trinidad species, and later with species of other countries. Where exchange of fungus gardens is attempted, a complication is the difference in pheromone substances of the two ant species, which the ants had added to the garden before the exchange; this difference may play a part in rejection. This complication is eliminated by using artificial cultures of the fungi (*19, 21, 29, 36, 41, 42*). Studies involving isolation of other fungi from laboratory colonies should be carried out (*27*). Rarely, conidial forms may develop (Fig. 13, *e* and *f*).

Moeller's *Rozites* has been reexamined taxonomically in recent years and is now referred to as *Leucocoprinus gongylophora* (*47*) or *Leucoagaricus* or *Agaricus gongylophora* (*48*). Meanwhile I developed the first sporophore or fruiting body of an ant fungus to be produced in the laboratory, by starting with the stage cultured by the ants (*29*) (Fig. 13*c*). This was considered to be a new species of *Lepiota* by Locquin. In 1965 W. J. Robbins and his associates produced what is apparently the same species of *Lepiota* but from a culture from another ant species, which I submitted to him. Heim (*47*) considered the first *Lepiota* to be the same as Moeller's. I believe this to be unlikely. If they were the same, we would have one species of fungus cultured by *Acromyrmex discigera* in south Brazil, by *Cyphomyrmex costatus* in Panama, and by *Myrmicocrypta buenzlii* in Trinidad. It is more likely that Moeller's species of fungus belongs to a group of similar species that are cultured by *Acromyrmex* and *Atta*. My tests of fungus cultures of a number of *Lepiota* species submitted by Robbins showed acceptances for eating (not culturing) by several attine species (*49*).

The other fungus genera of the 1938 review may be dismissed as follows.

The *Poroniopsis bruchi* Spegazzini from discarded substrate of *Acromyrmex (Moellerius) heyeri* and *Atta vollenweideri* is the same as *Hypocreodendron sanguineum* P. Henning (*50*). It has not been proved to be a true ant fungus. Another synonym is *Rhizomorpha formicarum* Spegazzini (loc. cit.). The new name *Discoxylaria mirmecophila* Lindquist and Wright applies (*51*).

The *Locellinia Mazzuchii* Spegazzini from a nest of *Atta vollenweideri* is considered to be a species of *Agaricus* (*47*). It is in the same category as *Lentinus atticolus* Weber 1938, not proved to be a true ant fungus. In both cases large mushrooms or sporophores were growing over ant nests. The fact that hyphae grew down to abandoned fungus gardens is not conclusive evidence that the fungus cultured by the ants was the same.

The *Xylaria micrura* of Spegazzini and, later, of Bruch is still not proved to be an ant fungus.

The *Tyridiomyces formicarum* Wheeler 1907 is still classified as a member of the Fungi Imperfecti since no sexual stage has been produced. It is the yeast cultured by *Cyphomyrmex rimosus* Spinola (Fig. 29). The hyphal stage shown in Fig. 29 is new and hitherto undescribed.

Additional ant fungi that I have developed from new sources are as follows.

1) The fungus cultured from a 1957 Panamanian colony of *Apterostigma mayri* Forel. A fructification developed in an oak flask culture; the culture was examined by Lekh Batra and submitted to G. W. Martin. The latter reported the fructification to be an *Auricularia*, perhaps *A. polytricha* (Mont.) Sacc., but, since it did not mature sufficiently, no further identification was possible.

2) The fungus cultured from a 1957 Panamanian colony of *Myrmicocrypta ednaella* Mann. A fructification developed in an oat flask culture but did not mature sufficiently for identification.

3) The fungus cultured from a 1957 Panamanian colony of *Cyphomyrmex rimosus* Spinola. Massive black sclerotia developed in a wheat flask culture; they were examined by W. C. Denison and Lekh Batra. The sclerotia were then sent to G. W. Martin, who characterized the subsequent culture and growth as that of a *Xylaria* with early similarities to *Daldinia*. The three mycologists agreed on its Ascomycetous nature.

In summary, the names presently applicable to ant fungi are as follows.

1) *Leucocoprinus, Leucoagaricus* or *Agaricus gongylophora* (Moeller 1893). Host ants: *Acromyrmex disciger*, possibly *Atta*.

2) *Tyridomyces formicarum* Wheeler 1907 (possibly a *Daldinia* or *Xylaria*). Host ant: *Cyphomyrmex rimosus*.

3) *Lepiota* n. sp. (Weber 1957, Robins 1965. Host ants: *Cyphomyrmex costatus, Myrmicocrypta buenzlii*.

4) *Auricularia* sp. Host ant: *Apterostigma mayri*.

Summary

Fungus-growing ants (Attini) are in reality unique fungus-culturing insects. There are several hundred species in some dozen genera, of which *Acromyrmex* and *Atta* are the conspicuous leaf-cutters. The center of their activities is the fungus garden, which is also the site of the queen and brood. The garden, in most species, is made from fresh green leaves or other vegetal material. The ants forage for this, forming distinct trails to the vegetation that is being harvested. The cut leaves or other substrate are brought into the nest and prepared for the fungus. Fresh leaves and flowers are cut into pieces a millimeter or two in diameter; the ants form them into a pulpy mass by pinching them with the mandibles and adding saliva. Anal droplets are deposited on

the pieces, which are then forced into place in the garden. Planting of the fungus is accomplished by an ant's picking up tufts of the adjacent mycelium and dotting the surface of the new substrate with it. The combination of salivary and anal secretions, together with the constant care given by the ants, facilitates the growth of the ant fungus only, despite constant possibilities for contamination. When the ants are removed, alien fungi and other organisms flourish.

A mature nest of *Atta sexdens* may consist of 2000 chambers, some temporarily empty, some with refuse, and the remainder with fungus gardens. Thousands of kilograms of fresh leaves will have been used. A young laboratory colony of *Atta cephalotes* will use 1 kilogram of fresh leaves for one garden. The attines are the chief agents for introducing organic matter into the soil in tropical rain forests; this matter becomes the nucleus for a host of other organisms, including nematodes and arthropods, after it is discarded by the ants.

One ant species cultures a yeast; all others grow a mycelium. In the higher species the mycelium forms clusters of inflated hyphae. Mycologists accept as valid two names for confirmed fruiting stages: *Leucocoprinus* (or *Leucoagaricus*) *gongylophora* (Moeller 1893) and *Lepiota* n. sp.

References and Notes

1. T. Belt, *The Naturalist in Nicaragua* (Murray, London, 1874).
2. A. Moeller, *Schimper's Botan. Mitt. Tropen* **6**, 127 (1893).
3. I. Huber, *Biol. Centralbl.* **25**, 606 (1905); *Smithsonian Inst. Ann. Rep.* **1907**, 355 (1907).
4. E. Goeldi, *Compt. Rend. Congr. Intern. Zool., 6th, Berne* (1905), p. 457; ———, *ibid.*, p. 508; ———, *Bol. Museu Nacl. Rio de Janeiro Geol. No. 5* (1908), p. 223; H. von Ihering, *Briefl. Mitt. Mundoro* **1**, 156 (1881); ———, *Berlin. Entomol. Z.* **39**, 321 (1894); ———, *Zool. Anz.* **21**, 238 (1898); A. G. Sampaio de Asevedo, *Saúva ou Manhúaára* (monograph) (São Paulo, 1894).
5. W. M. Wheeler, *Bull. Amer. Museum Nat. Hist.* **23**, 69 (1907).
6. E. Williams, *Documents of West Indian History* (PNM Publishing Co., Trinidad, 1963), vol. 1, 1492–1655; *History of the People of Trinidad and Tobago* (Praeger, New York, 1964).
7. Vernacular names for *Atta* are as follows. Cuba, *bibijagua*; Mexico, various, including *sonteta* and *hormiga arriera*; Central America, *zompopas*; Panama and Colombia, *hormiga arriera* or *podadora*; Venezuela, *bachaco*; Trinidad, *bachac*; British Guiana, *cuschi* or *acuschi*; Surinam, *parasolmieren*; Brazil, *saúva* or *saúba*, also *hormiga mineira, carregadeira*; Peru, *coqui*; Paraguay, *hormiga minera*; Uruguay and Argentina, *hormiga isaú*.
8. L. F. Byars, *J. Econ. Entomol.* **42**, 545 (1949); R. W. Neelands, *Forests and People* **1959**, No. 4, 1 (1959); C. P. Kennard, *Exp. Agr.* **1**, 237 (1965).
9. C. R. Gonçalves, *Divulgaçe Agron.* **1**, 2 (1960); ———, *Studia Entomol.* **4**, 113 (1961).
10. N. A. Weber, *Bol. Entomol. Venezuela* **6**, 143 (1947).
11. This role is emphasized in N. A. Weber, "Actas del Primer Coloquio Latinoamericano de Biología del Suelo" (Proceedings 1st Latin American Colloquium on Soil Biology) (UNESCO, Montevideo, in press).
12. Field work with students in Trinidad, W.I., in 1964 and 1965 was under the auspices of the National Science Foundation Undergraduate Research Participation Program. The students were Peter Delmonte, Stephen Hitchner, Mary Lewis, John Melbourne, Nancy and Peter Weber, and Gary Williamson. Various aspects of the study were aided by the Swarthmore Faculty Research Fund.
13. M. Autuori, *Rev. Entomol.* **11**, 215 (1940); *Arquiv. Inst. Biol. São Paulo* **12**, 197 (1941); ———, *ibid.* **3**, 67 (1942); ———, *ibid.* **18**, 39 (1947); ———, *ibid.* **19**, 325 (1950); ———, in *L'instinct dans le comportment des animaux et de l'homme* (Masson, Paris, 1956).
14. H. Eidmann, *Z. Angew. Entomol.* **22**, 185 (1935).
15. M. Bazire-Benazet, *Compt. Rend.* **244**, 1277 (1957).
16. W. E. Kerr, *Rev. Brasil. Biol.* **21**, 45 (1961).
17. A. A. Betancourt, *Arquiv. Inst. Biol. São Paulo* **12**, 229 (1941).
18. G. Stahel and D. C. Geijskes, *Rev. Entomol.* **10**, 27 (1939); ———, *ibid.* **11**, 766 (1940); ———, *ibid.* **12**, 243 (1941); ———, *Secr. Agr. Direc. Publ. Agron. São Paulo* (1943), p. 33; G. Stahel, *Ann. Primer Reun. Sul-Amer. Botan. Rio de Janeiro* (1938), vol. 1, p. 199; ———, *J. N.Y. Botan. Garden* **44**, 245 (1943). Sporophores growing wild from *Atta cephalotes* nests were considered by Stahel and Geijskes (1941) to be the same as *Rozites gongylophora*. Parts were cultured on nutrient agar, and staphylae appeared in 10 days. Stahel and Geijskes were unsuccessful in attempts to grow sporophores from these cultures. Dense fungal growths that did appear were removed from the sterile bottles and planted near ant nests. These degenerated or were cut and discarded by the ants. On other occasions conidial forms appeared in garden fragments of both *Atta cephalotes* and *A. sexdens*. In Surinam, as in south Brazil, sporophores that represent true ant fungi are exceedingly rare. Sporophores of unrelated fungi are not unusual. Whether any of the ant-nest-associated sporophores that were reported in the Argentine literature were indeed true ant fungi cannot now be ascertained, except in cases where it was found possible to rear viable spores from the original specimens.
19. N. A. Weber, *Rev. Entomol.* **17**, 114 (1946).
20. W. Weyrauch, *Bol. Direc. Gen. Agr. Peru* **15**, 204 (1942).
21. N. A. Weber, *Rev. Entomol.* **12**, 93 (1941); *Yearbook Amer. Phil. Soc.* (1956), p. 153.
22. M. Jacoby, *Rev. Entomol.* **6**, 100 (1936); *ibid.* **7**, 416 (1937); *Rev. Soc. Rural Brasil* **17**, 36 (1937); *Bol. Min. Agr.* **27**, 21 (1938); *ibid.* **32**, 55 (1943).
23. Trinidad subsurface temperatures under shade were taken by the method of N. A. Weber, *Ecology* **40**, 153 (1959), and were found comparable to temperatures for Panamanian *Atta*.
24. N. A. Weber, *Trop. Agr. Trinidad* **14**, 223 (1937).
25. J. C. Moser, *Ann. Entomol. Soc. Amer.* **56**, 286 (1963).
26. A. A. Bonetto, *Min. Agr. Ganad., Santa Fe, Argentina* (1959), p. 1; C. Bruch, *Ann. Soc. Cient. Argentina* **84**, 154 (1917); J. B. Daguerre, *Rev. Soc. Entomol. Argentina* **12**, 438 (1945); E. Lynch Arribalzaga, *Bol. Direc. Gral. Def. Agr. Argentina* (1910), p. 53; J. C. Otamendi, *Circ. Dept. Zool. Agr. Argentina* **17**, 11 (1945).
27. W. Goetsch, *Naturwissenschaften* **28**, 764 (1938); ———, *Tropenplanz.* **41**, 385 (1938); ———, *Zoologica* **35**, 1 (1939); ——— and R. Stoppel, *Biol. Zentr.* **60**, 393 (1940); W. Goetsch and R. Gruger, *Naturwissenschaften* **28**, 764 (1940); ———, *Rev. Appl. Mycol.* **20**, 257 (1941); ———, *Biol. Gen. Vienna* **16**, 41 (1942). South American colonies of *Atta sexdens* and *Acromyrmex striatus* were taken by Goetsch to Germany in 1938. He and Stoppel then repeatedly isolated *Hypomyces ipomoeae* and *Fusarium* spp. from the fungus gardens. The ants accepted these fungus species when they were in the company of other fungi, especially *Mucor*. Sugar juices were added, and the ants appeared to raise brood normally. The *Hypomyces* and *Fusarium* were said to thrive best in the saliva secreted by the ants. The saliva was toxic to other fungi. This interesting case does not alter the general conclusion that, in nature, an entirely different fungus has an obligatory relationship with the ants.
28. N. A. Weber, *J. Wash. Acad. Sci.* **45**, 275 (1955).
29. ———, *Ecology* **37**, 150 (1956); *ibid.*, p. 197; *ibid.* **38**, 480 (1957).
30. These castes were produced in the Swarthmore laboratory in colonies of known ages. The temperature was 24° to 26°C, and fungus gardens were maintained on fresh, leafy substrate. Autuori (*13*) found that *Atta sexdens* colonies were much older than *A. cephalotes* when soldiers first appeared.
31. H. Markl, *Science* **149**, 1392 (1965).
32. E. O. Wilson, *Ann. Rev. Entomol.* **8**, 345 (1963); *Science* **149**, 1064 (1965).
33. J. C. Moser and M. S. Blum, *Science* **140**, 1228 (1963); M. S. Blum, J. C. Moser, A. D. Cordero, *Psyche* **71**, 1 (1964); G. W. K. Cavill and P. L. Robertson, *Science* **149**, 1337 (1965).
34. V. A. Butenandt and B. Linzen, *Arch. Anat. Microscop. Morphol. Exp.* **48**, 13 (1959).
35. E. Amanta, personal communication to J. C. Moser (1965).
36. N. A. Weber, *Ann. Entomol. Soc. Amer.* **57**, 87 (1964).
37. ———, *Rev. Entomol.* **16**, 1 (1945).
38. W. M. Wheeler, *Mosaics and Other Anomalies in Ants* (Harvard Univ. Press, Cambridge, 1937).
39. Unpublished data from the Swarthmore laboratory.
40. N. A. Weber, in *Proc. Intern. Congr. Entomol., 10th, Montreal* (1958), vol. 2, p. 459.
41. ———, *Anat. Record* **125**, 604 (1956).
42. ———, *ibid.* **128**, 638 (1957).
43. ———, *Science* **121**, 109 (1955).
44. ———, *Anat. Record* **120**, 735 (1954).
45. W. M. Wheeler, *Ants* (Columbia Univ. Press, New York, 1926); A. Forel, *The Social World of the Ants Compared with Man* (Boni, New York, 1929).
46. N. A. Weber, *Rev. Entomol.* **8**, 264 (1938).
47. R. Heim, *Rev. Mycol.* **22**, 293 (1957).
48. R. Singer, personal communication (1965).
49. N. A. Weber, unpublished work.
50. J. C. Lindquist and J. E. Wright, *Darwiniana* **11**, 598 (1959).
51. ———, *ibid.* **13**, 138 (1964).